

## Zonal recovery after experimental displacement in two sea urchins co-occurring in the Mediterranean

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### Abstract

The difference in depth distributions of adult sea urchins *Arbacia lixula* L. and *Paracentrotus lividus* Lamarck (Echinodermata: Echinoidea) was assessed along a transect on a steeply and exposed stretch of the Tyrrhenian coast (Elba Island, Tuscany) in the four seasons of the year. *P. lividus* was always deeper zoned than *A. lixula* throughout the year, producing a consistent difference in the overall zonal pattern between the two sympatric species. The occurrence of a storm during the winter census had a marked effect on the zonation of *A. lixula* (consistent dislodgement and consequent downward shifting), while the distribution of *P. lividus* remained fairly unchanged. At a second, similar site along the Tyrrhenian coast (Argentario Promontory, Tuscany) experiments were conducted on individually marked sea urchins, which demonstrated the capacity of both species to move upward after experimental downward displacement. Only *P. lividus* also moved downward after experimental upward displacement. The study showed that the zonal segregation occurring between the two species along exposed rocky shores where they coexist is dynamically maintained against vertical diffusion and external perturbations related to water turbulence, by active movements allowing different adjustment of zonation pattern. © 1997 Elsevier Science B.V.

*Keywords:* *Arbacia lixula*; *Paracentrotus lividus*; Sea urchins; Zonal distribution; Zonal recovery

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### 1. Introduction

The two sea urchin *Arbacia lixula* L. and *Paracentrotus lividus* Lamarck are the most common echinoid species in the Mediterranean (Tortonese, 1965; Allain, 1975). Their ecology was extensively investigated by Kempf (1962) who reported differences in the

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depth distribution, microhabitat preference and dietary composition in populations co-occurring in the Gulf of Marseilles. Other informations on the depth distribution of the two species in Malta were also given by Neill and Larkum (1965) and by Gamble (1966). Lawrence (1975) discussed the competition between them, and the evidence for microhabitat and dietary segregation. Régis (1979) investigated the morphology of the test and the microstructural features of the skeleton of the two sea urchins in relation to their ecology. Taken together, these reports indicate that the two species usually select different areas of the shore along the sheltered-exposed gradient, as a result of their different resistance to hydrodynamics and, when coexisting, occur in different microhabitats. Particularly, when present on the same steeply and exposed coast, the two species adopt a different vertical zonation, with *A. lixula* dominant at the upper levels and *P. lividus* at deeper ones, where there is lesser water movement.

However, no information is available on movement patterns of the two species, and particularly on their capacity to maintain proper zonation against vertical diffusion or to recover it after displacement. Only some limited information on daily movements of *P. lividus* has been given by Ebling et al. (1966); Shepherd and Boudouresque (1979); Kitching and Thain (1983); Dance (1987). In the present study, we first considered the zonation patterns of the two species of sea urchins throughout one year along an exposed Tyrrhenian coast to assess the inter-specific differences in depth distribution under such conditions of exposure and substrate inclination; then, in a similar site, we tested their capacity for zonal recovery after experimental displacement toward shallower and deeper waters.

## 2. Methods

Two similar sites along the Tyrrhenian coast were selected for this study. The first, Punta Zanca, is a cape on the north-western coast of the Elba Island (Tuscany, 42°48' N; 10°12' E), where the high granitic shore runs steeply down to a sandy bottom (about 20 m depth). From the sea surface down to the sandy bottom a permanent transect 10 m wide was delimited using steel spikes driven into the rocky substrate. The transect was divided into horizontal belts using lines connected to the spikes. The first 9 belts (upper section) were laid on a relatively steep wall (0–9 m depth). Belts 10–11 (mid section) occurred on a gently sloping plateau between 9 and 11 m below the sea surface. Below the plateau (11–20 m depth, belts 12–20) there was a coralligenous wall again steeply sloping (lower section). Since the substrate varied in morphology and inclination along the transect, the surface area of the different belts was not constant.

Counts of the populations of the two species inhabiting the transect were conducted during four selected periods of the year: the second half of December 1991, the second half of March, June, and September 1992. During each census two SCUBA divers carefully inspected each belt, recording the species and size of each sea urchin encountered. Censuses were conducted during the night – when individuals of both species are better counted since usually outside shelters – and repeated during the day. Since no differences between nocturnal and diurnal depth distribution were observed in each species (except for the December censuses, when a storm occurred between the

nocturnal count and the diurnal one), only data from nocturnal counts were used to assess the interspecific difference in zonation. March, June and September counts were all conducted during periods of relatively calm sea. Sea urchins were assigned to different size classes according to their test diameter: in the present paper only zonation of larger class (test diameter > 30 mm) was considered.

The depth distributions of the adults of the two species were compared using the Wilcoxon-Mann-Whitney two-sample test (Siegel and Castellan, 1989) in each census.

The second site, Cala Piccola, was specifically used to test the ability of the two species to adjust their zonal position after experimental displacement. The study area is located on the western side of the Argentario Promontory (Tuscany, 42°26' N; 11°7' E). Here the calcareous coast runs steeply to 50 m below the sea surface, and the two species consistently inhabit the upper 20 m of this rocky wall. Adults of both species, living at depths between 3 and 15 m, were individually marked in October–November 1993. Individual marking was performed by passing a thin fishing line (0.35 mm in diameter) between the spines and fitting it close to the ambitus (i.e., around the equator of the test); a second short line bearing at one extremity a floating plastic tag (about 20 × 10 mm), individually numbered, was then fixed to the first one. This technique, similar to that used by Dance (1987), permitted efficient resighting of sea urchins.

The marked specimens of both species were divided into three groups: the control specimens (30 of each species) were left in place after marking; a second group (65 specimens of each species) was displaced downwards (from 3–5 m down to 25 m below sea surface), and a third group (59 *A. lixula* and 52 *P. lividus*) was displaced upward (from 13–15 m up to 3–4 m below the sea surface). The study area was later carefully inspected by two SCUBA divers and depth of marked sea urchins were recorded with an accuracy of 0.5 m about 20 days later. For each specimen the difference was then recorded between the depth at the beginning of the experiment and that recorded 20 days later. The depth distribution difference between the controls and experimentally displaced sea urchins was tested using the Wilcoxon–Mann-Whitney two-sample test (Siegel and Castellan, 1989).

### 3. Results

The depth distribution of adults of the two species in each season (nocturnal counts) is shown in Fig. 1, and the results of statistical comparisons between the depth distribution of the two species are shown in Table 1.

Although partially overlapped, the two species adopted a different pattern of zonation throughout all the year. *A. lixula* was more abundant than *P. lividus* in the upper section of the transect (0–9 m); the two species were equally represented in the mid part of the transect (9–10 m); the deeper part of the transect was inhabited almost exclusively by *P. lividus* which extended its zonation down to the base of the rocky slope. The large number of specimens of both species recorded between 9 and 10 m depends on the larger surface included in this belt due to gentler sloping, and to stronger irregularity of the substrate than in the rest of the transect.

No statistical comparison was performed between depth distributions of each species throughout the year, since the samples relative to the different counts were neither

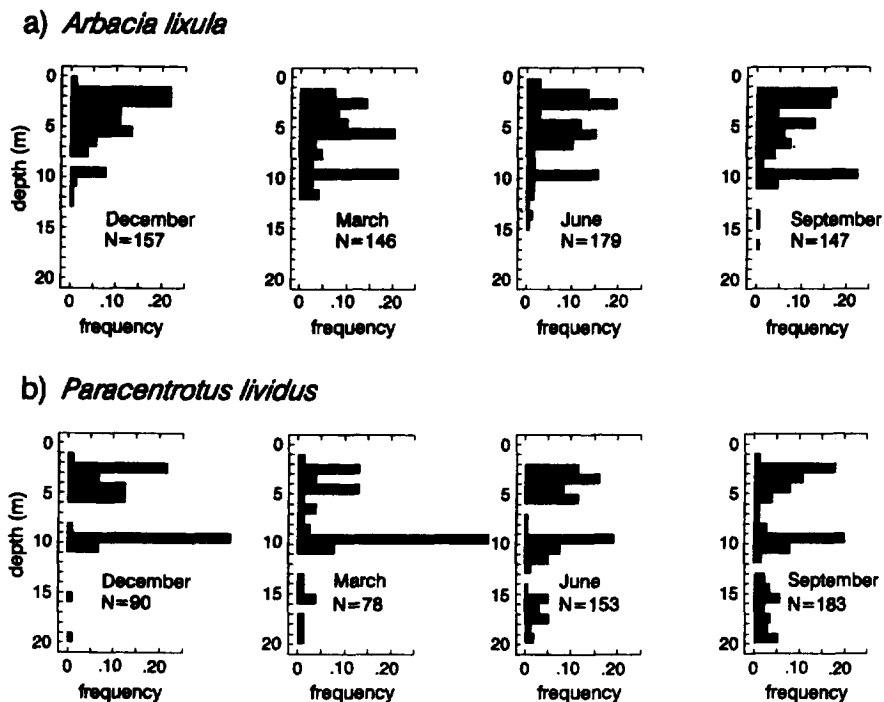


Fig. 1. *A. lixula* (a) and *P. lividus* (b). Frequency distributions of adult specimens at different depth along the transect of Punta Zanca, during the four nocturnal counts. *N*, sample size.

completely independent (most specimens were probably present in different counts) nor paired (identity of specimens was not assessed). However, the data suggest that the depth distribution of the two species was not completely stable during the year. Moreover, while the adult population of *A. lixula* was consistently stable in time, the presence of *P. lividus* varied with seasons: in June–September it was about double than in December–March.

A particular situation occurred during the December counts: in this case, while the nocturnal counts were performed during a period of relative calm sea, the daytime ones were conducted three days later, following a sea-storm of unusual intensity for that area. Adult *A. lixula* showed a marked downward shift if the depth distribution before and that after the storm are compared ( $4.7 \pm 2.7$  to  $6.5 \pm 2.7$  m average depth below the sea

Table 1

Results of the Wilcoxon-Mann-Whitney two-sample test for the comparison between the depth distributions of *Arbacia lixula* and *Paracentrotus lividus* adult classes during the four nocturnal censuses

December	March	June	September
$Z = 5.46$	$Z = 3.66$	$Z = 5.72$	$Z = 5.19$
$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$

Z, statistics of the Wilcoxon-Mann-Whitney test.

surface, respectively), while *P. lividus* showed a strong stability in depth ( $7.2 \pm 3.8$  and  $7.9 \pm 4.6$  m average depth, respectively). The depth difference before and after the storm was not statistically tested because data are neither completely independent nor paired.

The results of the experimental displacements were relatively clear. Control specimens of both species maintained their original zonation after about 20 days (C distributions in Fig. 2a and Fig. 2b). On the contrary, after downward displacement *A. lixula* showed an average upward movement of  $+1.95$  m (DD in Fig. 2a), while following the upward displacement this species did not show any evident zonal recovery ( $+0.07$  m) (UD in Fig. 2a). The comparison between downward displaced and control specimens was significant (Wilcoxon-Mann-Whitney test:  $Z = 4.833$ ,  $P < 0.001$ ), while that between upward displaced and controls was not ( $Z = 0.737$ ,  $P > 0.1$ ). A different pattern was evident in *P. lividus* (Fig. 2b): this species showed significant upward ( $+2.62$  m) and downward recovery ( $-0.78$  m) after experimental displacements, respectively: both distributions were statistically different from that of controls ( $Z = 5.997$ ,  $P < 0.001$  and  $Z = -3.674$ ,  $P < 0.001$ , respectively).

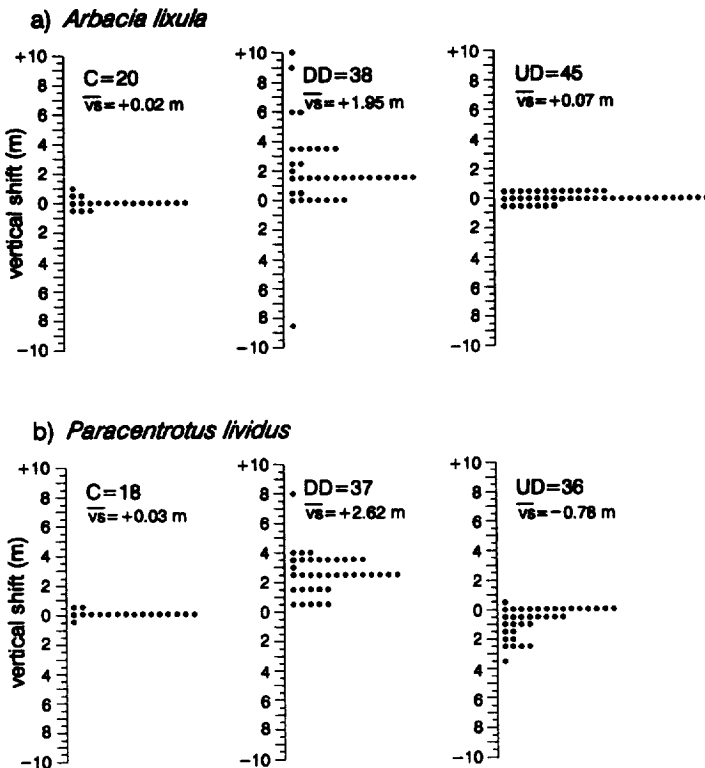


Fig. 2. *A. lixula* (a) and *P. lividus* (b). Results of displacement experiments conducted at Cala Piccola. Each dot represents the vertical shift of one specimen 20 days after the displacement: controls (C), downward displaced (DD), and upward displaced (UD). Sample size (resighted animals) is shown for each group.  $\bar{v}s$ , average vertical shift (positive, upward; negative, downward), taking the original depth as zero.

#### 4. Discussion

Firstly, our study confirmed, through counts replicated at different seasons, that adults of the two species, when coexisting on the same steeply and exposed rocky shore, have different depth distributions. This is consistent with previous reports in other areas of the Mediterranean sea (Kempf, 1962; Neill and Larkum, 1965; Gamble, 1966). That this different zonal pattern is actively maintained by the two species is suggested by their occurrence in the study area (particularly that of *P. lividus*) and their vertical distribution (both species) changing through the seasons. Moreover, it was evident from the effects of a storm which occurred during the winter counts, that high water-turbulence can modify consistently the zonal distribution of *A. lixula*.

It is often reported in the literature that hydrodynamics affect habitat selection in several species of sea urchins (Ebert, 1968; Littler, 1980; Monteiro Marques, 1982; Denny and Gaylord, 1996). Régis (1979), on the basis of a study of morphological and microstructural traits, concluded that *A. lixula* is more fitted than *P. lividus* to tolerate physical stress on its apical region. Its anatomical features would allow *A. lixula* to colonize the upper levels of the sublittoral in exposed areas, despite being subject to dislodgement by waves when storms of exceptional strength occur. On the contrary, *P. lividus* shows a distinct behavioural adaptation to wave action, by preferring deeper levels and occupying crevices and self-burrowed refuges. This might be the reason for the different effects of strong water turbulence on the zonation of the two species, as evidenced by our winter counts at Punta Zanca.

In the light of the above considerations it seems likely that zonal recovery exhibited by *A. lixula* after downward experimental displacement has evolved as a behavioural adaptation to dislodgement by waves, and consequent falling into deeper waters in steep exposed rocky coasts. Interestingly, however, also *P. lividus* exhibits such upward response after downward displacement. This could mean that also this species can be occasionally subjected to dislodgement by waves, or the active recovery of shallower waters might be a mechanism counterbalancing the downward diffusion during natural movements (e.g. for foraging). Our experiments showed that only *P. lividus* exhibits a downward recovery after upward experimental displacement, showing an active avoidance of upper levels in steep exposed areas. Again, this response could have been evolved to counterbalance long term upward diffusion of *P. lividus* when actively moving. Hence the results of our experiment suggest that the two sea urchins show active orientation for the zonal maintenance against displacement or vertical diffusion. This orientation capacity is widespread among coastal animals, both invertebrate and vertebrate, involving a variety of releasing and orienting stimuli (Jander, 1975; Pardi and Ercolini, 1986; Chelazzi, 1992). However, similar studies were lacking on echinoids: the only previous paper dealing with this particular subject in echinoderms is that of Pabst and Vicentini (1978), showing seasonal zonal migration and zonal recovery after experimental displacements in the soft bottom asteroid *Astropecten johnstoni*. Which factors trigger the zonal adjustment of *A. lixula* and *P. lividus*, and the orienting cues involved in their zonal orientation remain to be assessed. We can only speculate that water turbulence, pressure and spectral composition of the light might be the candidate factors for eliciting zonal adjustment, while geotaxis may account for their correct vertical orientation.

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